植物分类学报
第21卷 第3期 ACTA PHYTOTAXONOMICA SINICA 1983年 8月

蔷薇科太行花属系统位置的研究

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我们在确立太行花 *Taihangia* Yü et Li 这一新属的同时，对该属植物作了多方面的研究工作，包括形态学、心皮解剖、染色体观察以及花粉的光学、扫描和透射电子显微镜等分析工作，并与其相近类群作了比较。此外，还对该属种内两个变种作了同工过氧化物酶谱比较，以便根据多种特性探讨该属在蔷薇科中的演化系统位置。现将初步结果报告如下：

一、材料和方法

本文研究使用的各属植物材料大多采自中国科学院植物研究所标本室的腊叶标本；部分新鲜材料采自河北省武安和河南省林县。在进行属间比较时，我们不可能将每一个属的全部种类都取来进行研究，只能抽样式地选择其中的代表类型。选取种类的原则是：单种属，选模式种；少种属则依据其种间分化的式样选取类型分化的代表种 1 至数种；多种属则选取进化上比较原始、中等和高等的不同类型；同时，种类如分布各大洲，则注意配合选择分布在不同洲的代表，尤其分布在欧亚和美洲的都要有代表；此外，还要注意选取属间的临界种。

心皮解剖：子房经蒸馏水浸透，用氢氟酸软化表皮毛，纳瓦兴固定液固定，按一般石蜡制片法进行制片。

染色体观察：用新鲜芽叶，秋水仙碱预处理，卡诺氏液固定，浮尔根染色。镜检体细胞染色体。

花粉光学显微镜观察：按 Erdtman（1943）醋解法处理，光学树脂胶固封，镜检。

花粉表面扫描电镜观察：醋解法处理后，花粉分别放于已编号的金属标本台胶带上，真空镀膜机喷镀，镜检用 S4-10 型扫描电镜。

花粉壁透射电镜观察：醋解法处理后，用锇酸固定，水洗，琼脂浓缩，酒精及环氧丙烷逐级脱水，812# 包埋剂浸透包埋，60℃ 聚合 24 小时，80—90℃ 保温 2 小时，超薄切片，醋酸双氧铀和柠檬酸铅染色，镜检用日制 HU-11A 或 JEM-1000CX 型透射电子显微镜。

同工过氧化物酶谱比较：新鲜根状茎下部和根 1 克，加 10 毫升含 20% 蔗糖 pH5 的

本文工作涉及到分类、解剖、细胞、孢粉和生化等五个分支学科的技术手段。我们曾在中国科学院植物研究所分类室、形态室、古植物室（孢粉组）、光合室（结构组）和固氮室等五个研究室进行过工作，我们十分感谢这些研究室的负责人给予我们的支持。特别要感谢常永祯、席以珍、徐庭玉、左宝玉、李世仪、张芝玉、王中仁、顾立明和胡志昂等同志，和中国科学院生物实验中心傅广礼、吴莲英和及惠芬同志，北京石油勘探开发科学研究院唐黎平和李维民同志给予我们的大力援助。感谢中国科学院植物研究所孟昭义同志、中国科学院成都生物研究所赖坚等同志在洗印照片方面给予的援助。我们这篇综合分析研究的初步成果，应归功于以上多位同志的关心和支持。

0.2*M* 醋酸钠缓冲液，低温（约 −2℃）在研钵中研成糊状。两层纱布过滤，滤液经 2000g 离心 10 分钟，上清液即为酶液，贮于冰箱中备用。聚丙乙烯酰胺凝胶垂直板电泳采用 Davis（1964）缓冲系统，但不用样品胶，含蔗糖的样品液直接加在间隔胶上槽内。在冰箱中 250—300 伏电压下稳压电泳 3—4 小时，后取出胶板，去间隔胶，用愈创木酚法（Mader et al., 1975）显示同工过氧化物酶。

二、观察和结果

外部形态学：本属植物主要特点是多年生草本。单叶，稀在叶柄上部有 1—2 退化裂片。单花顶生，稀 2 朵，着生在无叶的花葶上，花葶上有 1—5 个不孕的苞片，雄花和两性花同株或异株；萼片和副萼片各 5；花瓣 5，白色；雄蕊多数；雌蕊多数，在雄花中数目较少，败育，无毛(图版 2:5—6)，在两性花中数目较多，螺旋状着生在延长的花托上，花柱延长，被稀疏短柔毛。

与仙女木族各属相比较，从草本习性尤其是花开始出现单性来看，太行花属是比较进化的。从花柱的类型来看却比较原始，本属植物花柱虽然伸长，但花柱上的毛细而短。其他如仙女木属 *Dryas* L. 花柱被毛较长形成羽毛状，高度适应于风传播；路边青属 *Geum* L. 则花柱有关节，果期顶端脱落，宿存部分顶端呈钩状，高度适应于动物附着传播；林石草属 *Waldsteinia* Willd. 无尾果属 *Coluria* R. Br. 等花柱完全脱落，果实有时表面有腺体或光滑，适于蚂蚁或其他小昆虫搬运传播(图版 1:1—8；图版 2:1—4)。

心皮解剖表明，太行花属胚珠基生倒转（图版 2:12)，若与蔷薇亚科具有下垂胚珠的各族相比较，显示出本属植物与仙女木族各属植物同处于一条进化线上；子房连续横切面显示，腹背维管束在子房基部分离（图版 2:7—11)，说明比较原始，而在仙女木和路边青等属则在子房基部融合，比较进行。按 Chute（1930）和 Sterling（1953, 1969）等人的研究，瘦果心皮维管束演化伴随着背腹维管束融合和退化。

染色体观察：体细胞染色体 2n = 14，染色体基数 x = 7（图版 3:3)。在风传播和动物附着传播的草本植物属中，二倍体植物的属还是首次发现，从这个角度来看，本属植物比较原始，说明它是草本植物中比较古老的残余属，在本族植物进化上具有重要意义。太行花及其近缘属的染色体倍性及其基数比较如下：

仙女木属 *Dryas* L. 2x(x = 9)，木本，花柱呈羽毛状，靠风传播；太行花属 *Taihangia* Yü et Li 2x(*x* = 7)，草本，花柱伸长，毛短，靠风传播；林石草属 *Waldsteinia* Willd. 2x, 6x(x = 7)，草本，花柱完全脱落，靠蚂蚁或其他小昆虫搬运传播；无尾果属 *Coluria* R. Br. 2x(x = 7)，草本，花柱完全脱落，靠蚂蚁或其他小昆虫搬运传播；羽叶花属 *Acomastylis* Greene 6x, 8x(x = 7)，花柱几乎不延长，基部有毛，靠风传播；路边青属 *Geum* L. 6x, 10x, 12x(x = 7)，花柱顶部有关节，脱落后顶端呈钩状，靠动物附着传播。

据 Sax（1930), Gajewski（1957）和 Stebbins（1950, 1971）等人的研究，在蔷薇科植物的染色体基数 x = 7、x = 8、x = 9中，x = 9 是最原始的，其次是 x = 8、x = 7 是晚进的。前两者大多表现在木本植物中，晚进者大多表现在草本植物中。植物从木本进化到草本的过程中，染色体的基数以非整倍性递降的方式产生了如下进化路线：$x = 9 \to x = 8 \to x = 7$。并且在同一基数水平上，再由二倍体植物进化产生多倍体植物。根

据这种解释，太行花属比木本植物仙女木属（x = 9）更进化，比草本植物如羽叶花和路边青等属原始，虽然它和后面两个属染色体基数相同，但是后面这些属都是多倍体。与无尾果和林石草属比较，虽然都具同一的染色体基数，并且都是具有二倍体的植物，可是它们脱落的花柱和依靠蚂蚁等小昆虫传播的方式是相当进化的。它们之间这种形态学分化的巨大差异，并不表现在染色体倍性的变化上，而很可能表现在染色体个体或基因水平上，这有待进一步研究。

光学显微镜和扫描电镜显示的花粉形态特征表明，本属植物的花粉为椭圆球形，具三孔沟（图版 3:4—15）。扫描电镜中清晰可见有两型花粉，一种类型外壁表面呈皱波状，而另一类型表面有短或稍长而狭的条纹。与仙女木族其他属比较，仙女木属也有两型花粉，一种类型也具短条纹，但较粗，而另一类型却显示出大小不等的粗短条纹；与路边青、羽叶花、无尾果和林石草等属比较，孔沟类型十分相近，但这些属的外壁雕纹大多是沿子午线平行分布的长条纹，未见有两型花粉（图版 4—6）。

对太行花及其近缘属植物代表种花粉壁进行了透射电镜研究，结果显示（图版 7:1—9），它们的外壁明显分成内外两层(外壁分层类型按 Walker, 1976)：外壁外层包括覆盖层和柱状层；外壁内层，看来仅由染色较浅的部分构成(图 1)，在萌发孔及其附近明显加厚，不存在基层。从覆盖层特点来看，有三种不同的类型（图 1)：太行花、羽叶花、路边青、无尾果和林石草等属具无穿孔覆盖层(图 1:A)，覆盖层上雕纹分子顶端尖锐的有太行花、路边青和林石草等属，覆盖层上雕纹分子顶端钝头的有羽叶花和无尾果等属，两者基部均较宽阔；木本的仙女木属花粉在超薄切片图象上显示出两型现象，一种类型具半覆盖层，是处于穿孔覆盖层和无覆盖层之间的一种类型（图 1:C)，覆盖层上的雕纹分子呈棒形，顶端圆钝头，基部等大或常微缩小；另一种类型具穿孔覆盖层(图 1:B)，覆盖层上雕纹分子不等大，有的较粗而长，有的较细而短。

据初步观察，草本植物和木本植物的属，是分别沿着不同方向发展的。太行花属花粉的超薄切片图象也显示出它与其他草本植物属的近缘关系。但是太行花属与其近缘草本属相比较，特别的是存在的两型花粉，在超薄切片图象上也显著地表现出来：一种类型花粉壁呈皱波状，图象上显示雕纹分子顶端宽阔平钝或微凹，与基部近相等；另一种类型花粉壁图象显示的雕纹分子具尖锐的棱背。

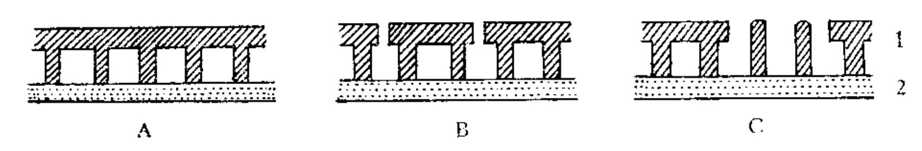


图 1　花粉外壁示意图：A. 无穿孔覆盖层；B. 穿孔覆盖层；C. 半覆盖层。
(1. 外壁外层，2. 外壁内层)

三、讨　论

根据上述观察和比较分析，我们不仅可以对该属植物的系统位置进行初步评价，而且还能为阐明该属与其近缘属之间的进化提供一些线索。

蔷薇科的果实分化多种多样，过去学者常用作分亚科的主要特征之一。事实上，果实

的传播方式在蔷薇科的繁衍上起着重要作用，最原始的是蓇葖果，而瘦果、核果和梨果是后进的。瘦果在蔷薇亚科中是基本的特点，尤其是在仙女木族中，果实传播的方式显著向三个不同的方向发展，同时在花柱形态上也发生相应的特化：依靠风传播，如仙女木属，具有高度发展的羽毛状长花柱；依靠蚂蚁等小动物搬运传播，如无尾果和林石草属，花柱脱落，有时果实上有腺体或光滑无毛；依靠动物附着传播，如路边青属，花柱顶端有关节，果期脱落，宿存部分呈钩状。太行花属是处于中生性的华北森林植物区系内中国特有的属，由于它生长的特定生境，加上非羽毛状的花柱，既不完全高度适应风传播，也不适应动物附着传播，因而具有狭小的分布区而成残遗状态。所以该属可能是风传播植物祖先的直接后代。从保持了植物的二倍体特性来看，本属植物的祖先可能是代表了风传播和动物传播之间的联系。

多年来，若干植物细胞分类学家，在仙女木族的草本风传播和动物附着传播的研究中，发现的都是多倍体的属种类植物，而原始二倍体属种类的植物却仅在我国太行山区发现。从二倍体植物大多分布在起源中心，而多倍体植物是在扩大分布区中形成，多分布在起源地区的边缘这一论点出发，因此推论东亚特别是山区可能是仙女木族中草本的风传播和动物附着传播植物属种的起源中心之一。

总之，太行花属的各种特性，如花柱状态、心皮维管束系统和保持了二倍染色体特性等是原始的；有的则是特化的，如花性别上除两性花外还发展有单性（雄性）花，这在其近缘属中是没有的。由此看来它是本族草本植物属中最原始的，在仙女木族进化上占有特殊的位置，现设想其进化路线与系统关系如图 2。

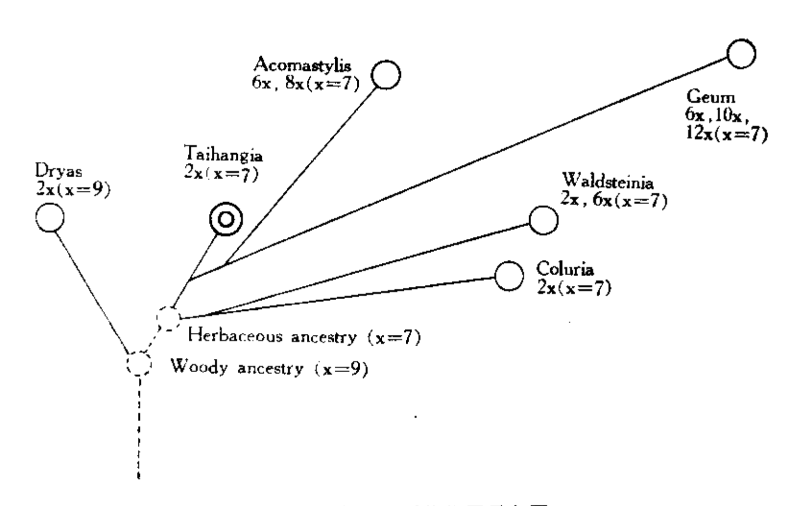


图 2 太行花属系统位置示意图

Hypothetical systematic position of the genus *Taihangia* and its related groups

此外，我们仅就采集标本时到过的地段，将收集到的活植物带回，对两个变种进行了同工过氧化物酶的比较分析，显示出两个变种的差异：原变种有六个主带 (A, B, C, D, E, F)，变种有四个主带(A, B, C, G)其中三个主带 (A, B, C) 相同；原变种有三个特有的带 (D, E, F)，变种有一个特有带(G)(图版 3：1—2)。我们在实验过程中，对根、根状茎和叶片作了同工过氧化物酶检测，发现根和下部根状茎酶活性最高，上部根状茎次之，叶片

几乎没有；所以上述实验是用新鲜的根和下部根状茎提取出来的酶液电泳得出来的酶谱作比较分析的。由于结构基因编码同工酶，所以酶谱中带数的差异，表型出了结构基因数目的差异。虽然，我们采集的居群数目有限，远不能就此得出一个完整的结论，但是我们目前就是根据这些实验材料相对应的标本来进行分类的，因此就这些实验材料来说，支持了这两个变种的划分。

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THE SYSTEMATIC POSITION OF GENUS *TAIHANGIA* IN ROSACEAE

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Summary

We have described a new genus *Taihangia,* collected from the south part of Taihang Mountain in northern China. At the same time, comparative studies on *Taihangia* with its related genera have been made in various fields including external morphology, anatomy of carpels, chromosome and pollen morphology by light, scanning and transmission electron microscope. In addition, isoperoxidases of two varietier were analysed by means of polyacrylamide gel slab electrophoresis. The preliminary results are as follows:

Morphology: The genus *Taihangia* is perennial and has simple leaves, occasionally with 1—2 very small reduced lobes on the upper part of petiole; flowers white, andromonoecious and androdioecious, terminal, single or rarely 2 on a leafless scape; calyx and epicalyx with 5 segments; petals 5; stamens numerous; pistils numerous, with pubescent styles,

spirally inserted on the receptacle in bisexual flowers, but with less number of abortive and glabrous pistils in male flowers.

In comparison with the related genera such as *Dryas, Geum, Coluria* and *Waldsteinia*, the new genus has unisexual flowers and always herbaceous habit indicating its advanced feature but the genus has a primitive style with thin and short hairs as compared with the genus *Dryas* which has long, pinnately haired styles, a character greatly facilitatng anemochoric dissemination. The styles of *Taihangia* are slender and differ from those of the genus *Geum* which are articulate, with a persistent hooked rostrum, thus adapting to epizoochoric dissemination to a higher degree.

The anatomy of carpels shows the baral position of ovules in the genus *Taihangia* like those in other related genera such as *Dryas, Geum, Acomastylis, Coluria* and *Waldsteinia*. This suggests that the new genus and its related ones are in a common evolutionary line as compared with the other tribes which have a pendulous ovule and represent a separate evolutionary line in *Rosaceae*. Dorsal and ventral bundles in carpels through sections are free at the base. Neither fusion, nor reduction of dorsals and vertrals. are observed. This shows that the genus *Taihangia* is rather primitive.

Somatic chromosome: All the living plants, collected from both Honan and Hopei Provinces were examined. The results show that in these plants the chromosome number is $2n=14$, and thus the basic number of chromosome is $x=7$. Such a diploid genus is first found in both anemochoric and epizoochoric genera. Therefore, in this respect *Taihangia* is primitive as compared with herbaceous polyploid genus *Geum* and related ones.

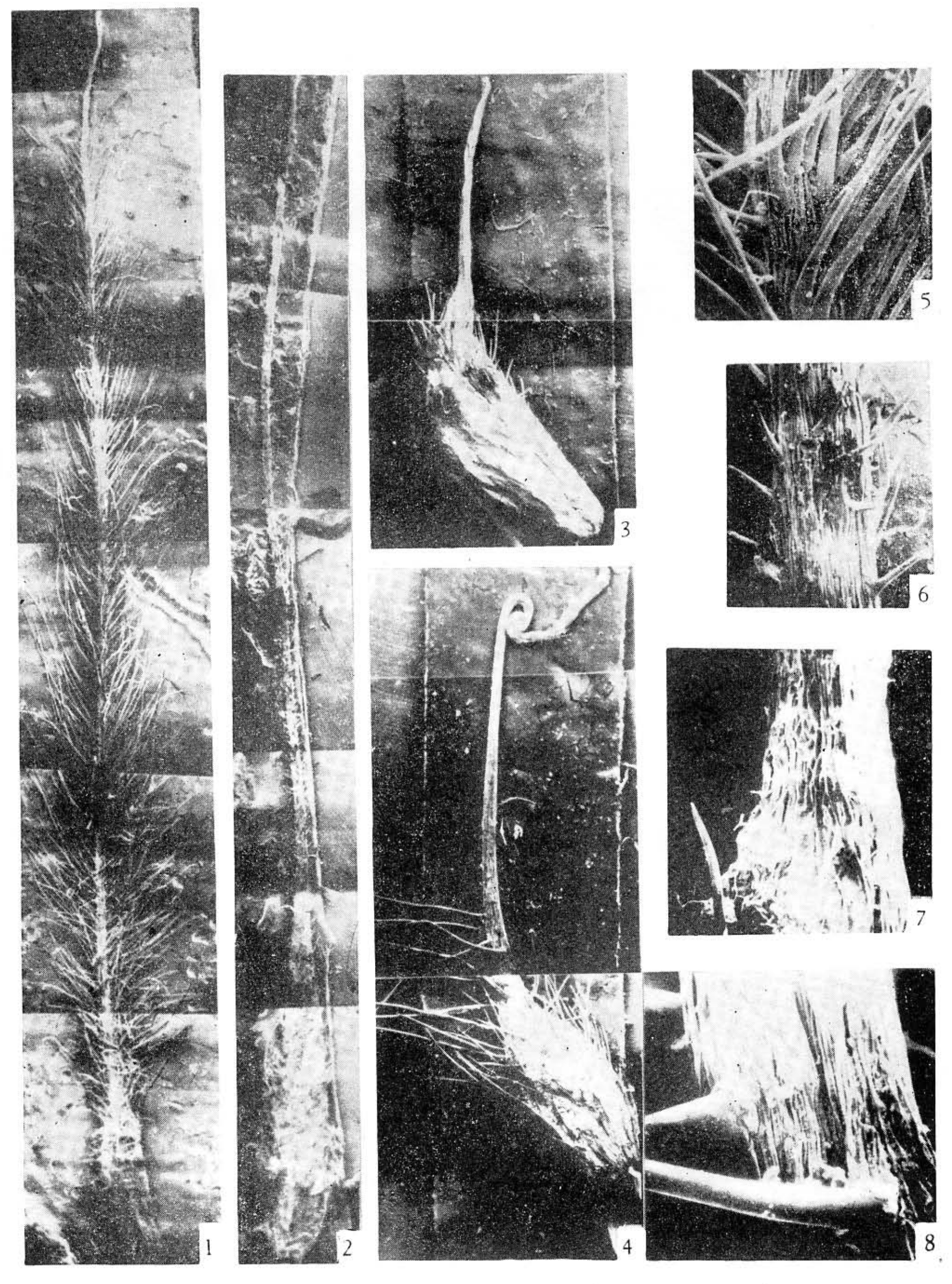
Pollen: The stereostructure shown by scanning electron microscope reveals that the pollen grains of the genus *Taihangia* are ellipsoid and 3-colporate. There are two types of exine sculpture. One is rather shortly striate and it seems rugulate over the pollen surface; the other is long-striate. The genus *Dryas* differs in having only short and thick striae over the surface. The genus is similar to the genera *Geum, Coluria* and *Waldsteinia* in colpus type, but differs from them in that they all have long, parallel striae which are distributed along the meridional line.

In addition, under transmission electron microscope, the exine in the *Taihangia* and related genera *Acomastylis, Geum, Coluria, Waldsteinia* and *Dryas* has been shown to be typically differentiated into two distinct layers, nexine and sexine. The nexine, weakly stained, appears to consist of endoxine with no foot-layer, in which the columellae are fused, and which is thicker beneath the apertures. The sexine is 2-layered, consisting of columellae and tectum. Three patterns of tectum can be distinguished in the tribe *Dryadeae:* the first, in the genera *Taihangia, Acomastylis, Geum, Coluria and Waldsteinia,* is tectate-imperforate, with the sculpturing elements both acute and obtuse at the top and broad at the base; the second, in the genus *Dryas,* is semitectate, with the sculpturing elements shown in ultrathin sections rod-like and broader at the top than at the base or as broad at the top as at the base, and the third, tectate-perforate, with the sculpturing elements different in size. From the above results, the herbaceous groups and woody ones have palynologically evolved in two distinct directions, and the genus *Taihangia* is related to other herbaceous genera such as *Acomastylis, Geum, Coluria* and *Waldsteinia,* as shown in the electron microphotographs of ultrathin sections. The genus *Taihangia,* however, is different from related herbaceous genera in that the pollen of *Taihangia* is dimorphic, i.e. in addition to the above pattern of pollen another one of the exine in *Taihangia* is rugulate, with the scul-

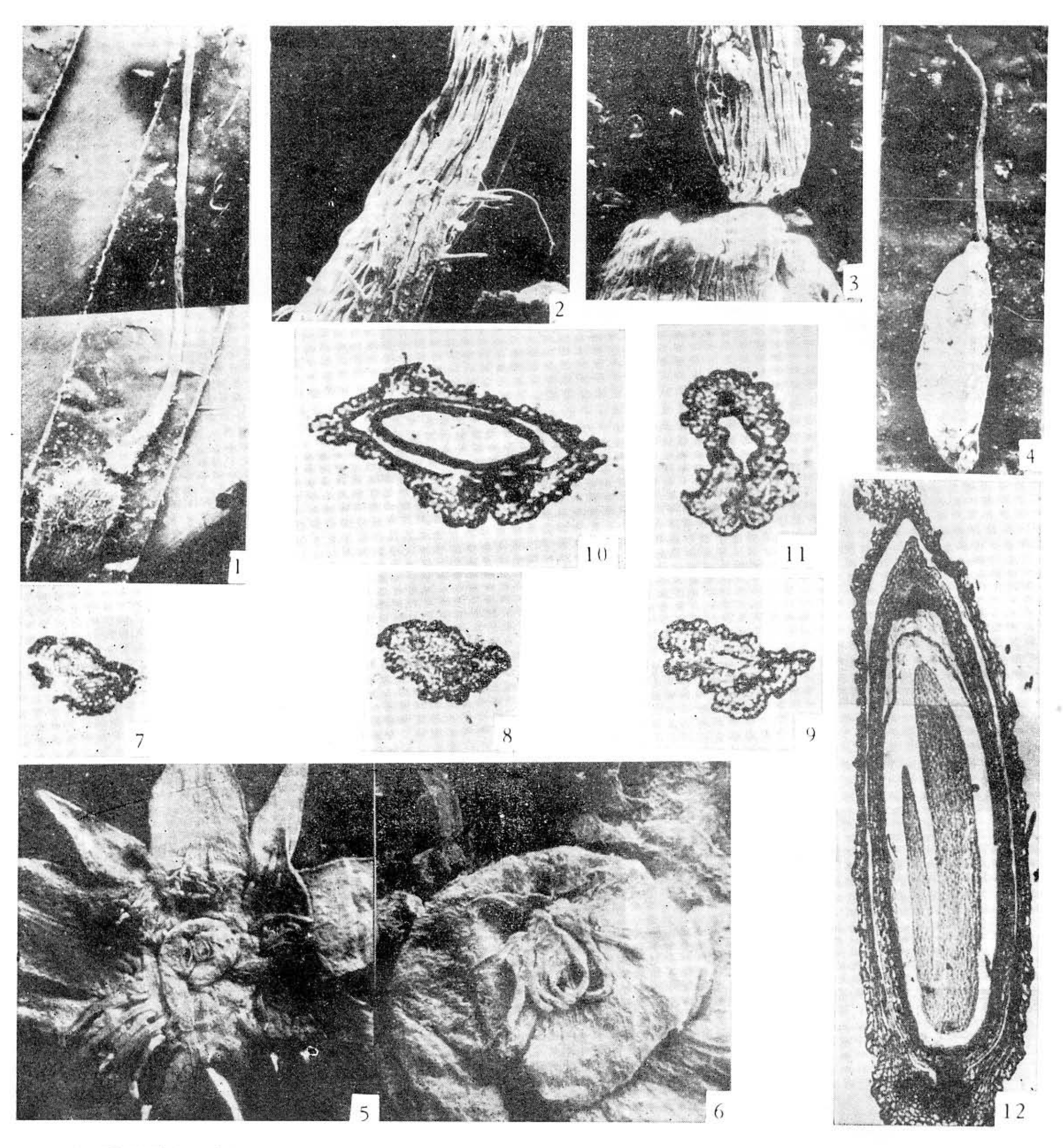
pturing elements shown in the ultrathin sections being obtuse or emarginate and nearly as broad at the top as at the base.

The interesting results obtained from the comparative analysis of morphology, anatomy of carpels, chromosome countings, microscopic and submicrosocopic structures of pollen may enable us to evaluate the systematic position of *Taihangia* and to throw a new light on evolution of the tribe *Dryadeae*. It is well known that the modes of dissemination of rosaceous fruits play an important role in the expansion and evolution of the family. The follicle is the most primitive and the plants with follicles, like the *Spiraeoideae*, are mostly woody and mesic, while the achene, drupe and pyrenarium are derived. In *Rosoideae* having a achene is a common feature. Particularly in the tribe *Dryadeae*, which is distinguished from the other related tribes by having orthotropous ovules, te methods of dissemination of fruits have developed in three distinct specialized directions: anemochory with long, plumose styles (e.g. *Dryas*), formicochory or dispersed by ants or other insects, with the deciduous styles (e.g. *Waldsteinia* and *Collria)*, and epizoochory with the upper deciduous stigmatic part and the lower persistent hooked rostrum, an adhesive organ favouring epizoochory dissemination (e. g. *Geum* and related taxa). *Taihangia* is a genus endemic to mesophytic forest area of northern China. Due to its narrow range and specific habit as well as pubescent styles, neither perfectly adapted to anemochory nor to epizoochory, the genus *Taihangia* might be a direct progeny of the ancestry of anemochory. Maintaining the diploidy and having an ntermediate sculptural type of pollen, the new genus might probably represent a linkage between anemochory and zoochory (including epizoochory and dispersed by ants).

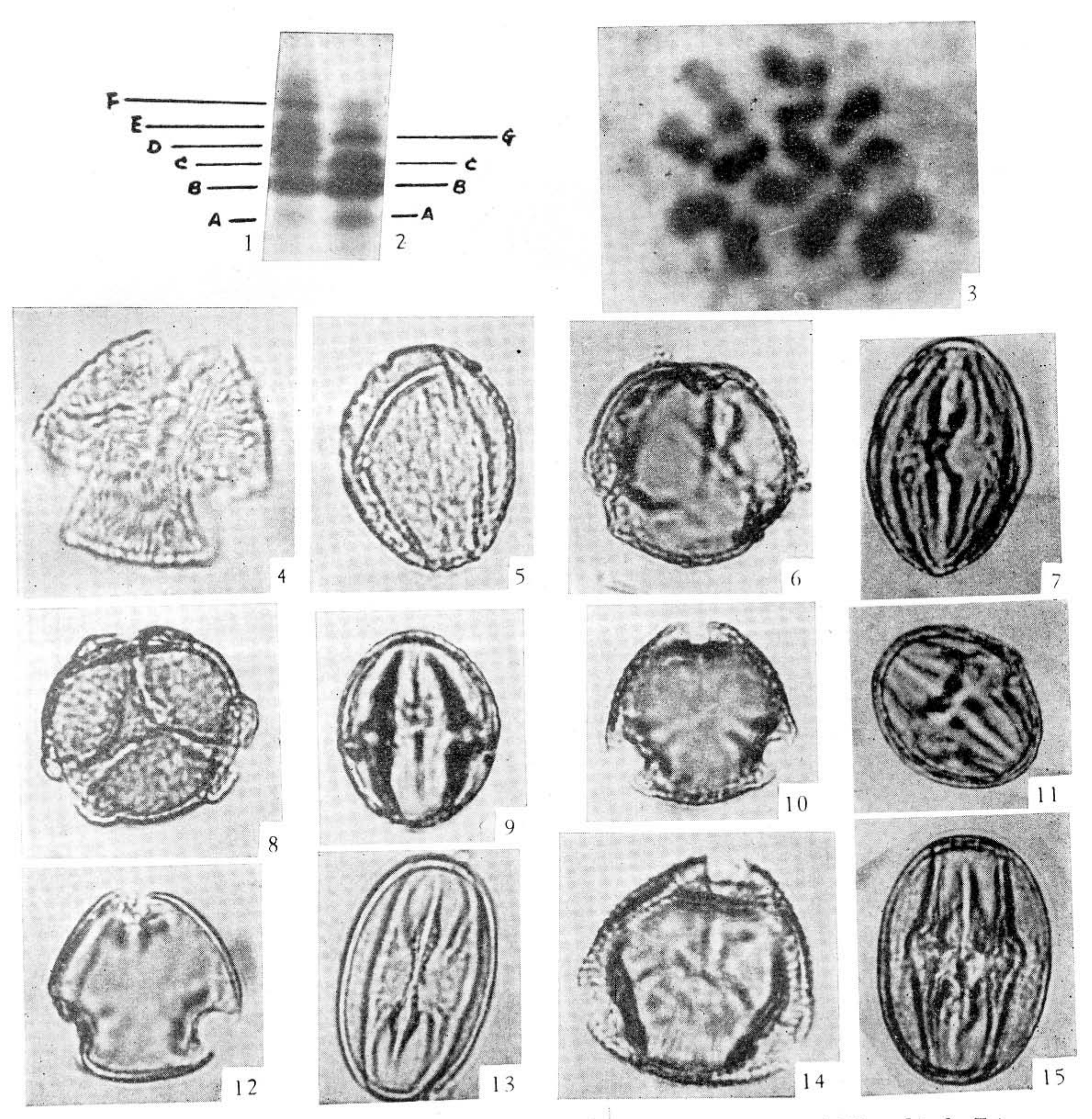
Experimental evidence from isoperoxidases shows the stable zymograms of root and roostoks. The anodal isozyme of *T. rupestris* var. *rupestris* may be divided into 6 bands: A, B, C, D, E, F, and *T. rupestris* var. *ciliata* into 4 bands: A, B, C, G. The two varieties of the species share 3 bands: A, B, C. However, D, E and F bands are characteristic of var. *rupestris* and G band is limited to var. *ciliata*. As far as the available materials are concerned, the analysis of isoperoxidases supports the subdivision of the species into two varieties.



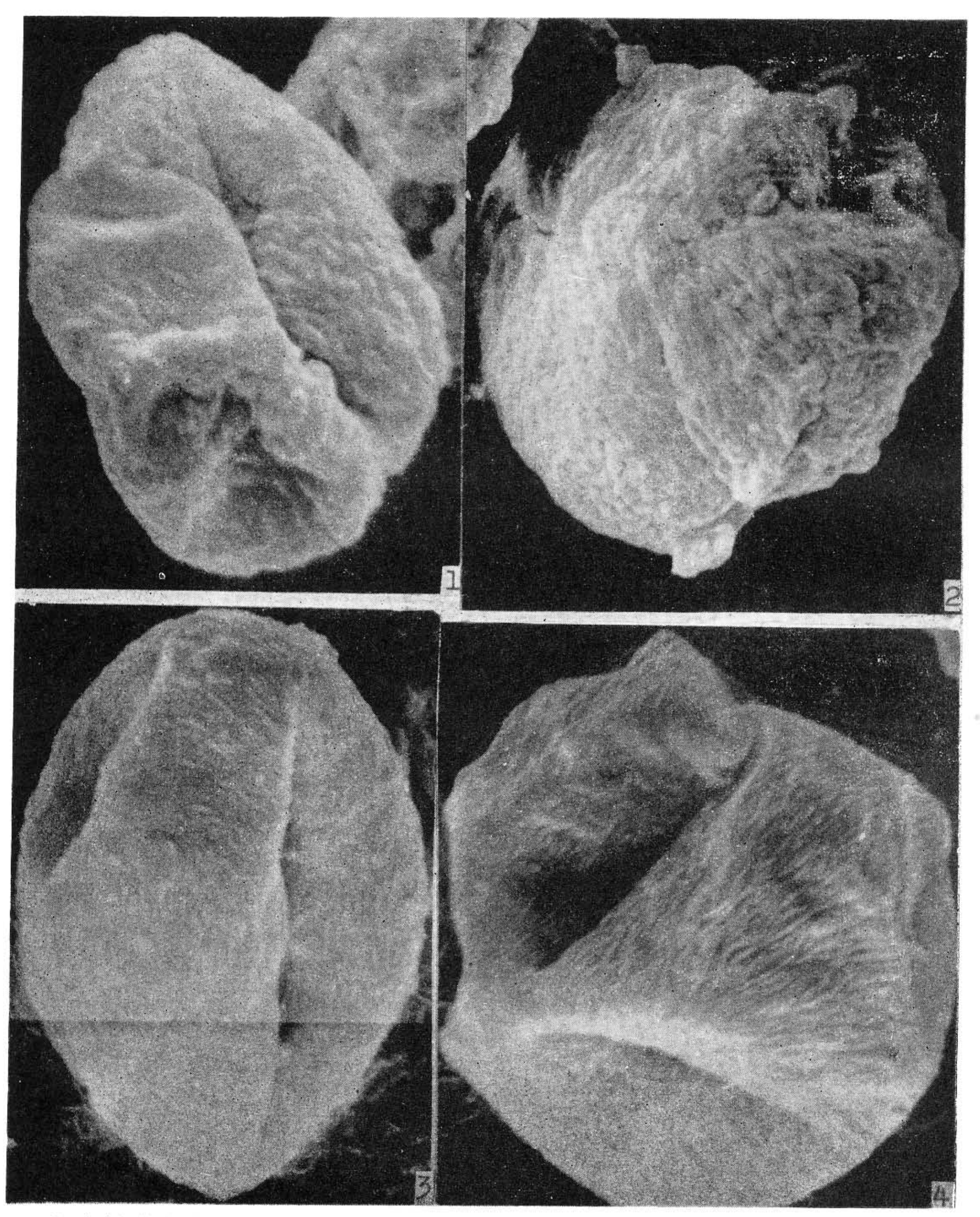
1—8. 雌蕊扫描电镜照片 SEM photographs of pistils 1,5. *Dryas octopetala* var. *asiatica* Nakai; 2,6. *Taihangia rupestris* Yü et Li; 3,7. *Acomatylis elata* var. *leiocarpa* (Evans) F. Bolle; 4,8. *Geum japonicum* var. *chinense* F. Bolle (1—4. 整体雌蕊 the whole pistils ×12; 5—8. 部分花柱 the parts of styles ×120).



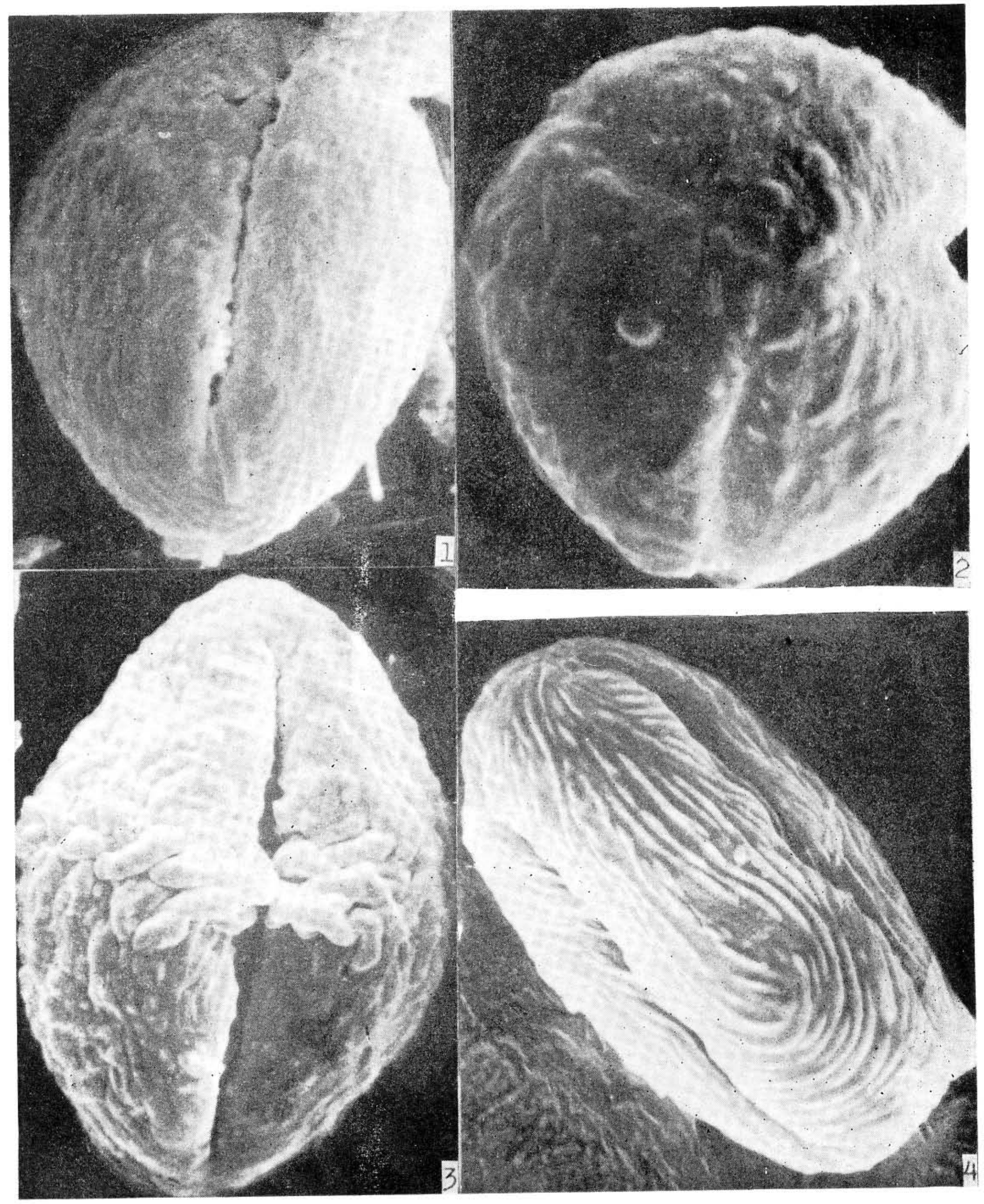
1—12 雌蕊和心皮扫描电镜照片 SEM photographs of pistils and carpels 1—2. *Waldsteinia ternata* (Steph.) Fritsch; 3—4. *Coluria longifolia* Maxim. (1,4. 整体雌蕊 the whole pistils ×12; 3,4. 部分花柱 the parts of styles ×120); 5—6. *Taihangia rupestris* Yü et Li; 5. 雄花 male flower ×6.5; 6. 雄花中败育雌蕊 the abortive pistils ×17; 7—11. 太行花心皮横切面 Transections of carpel of *Taihangia*; 7—9. 心皮基部(示背腹维管束分离) at the base (dorsal and ventral bundles free); 10. 心皮中部 at the middle; 11. 心皮顶部 at the top c.×80; 12. 太行花心皮纵切面 longitudinal section of carpel of *Taihangia* c.×32.



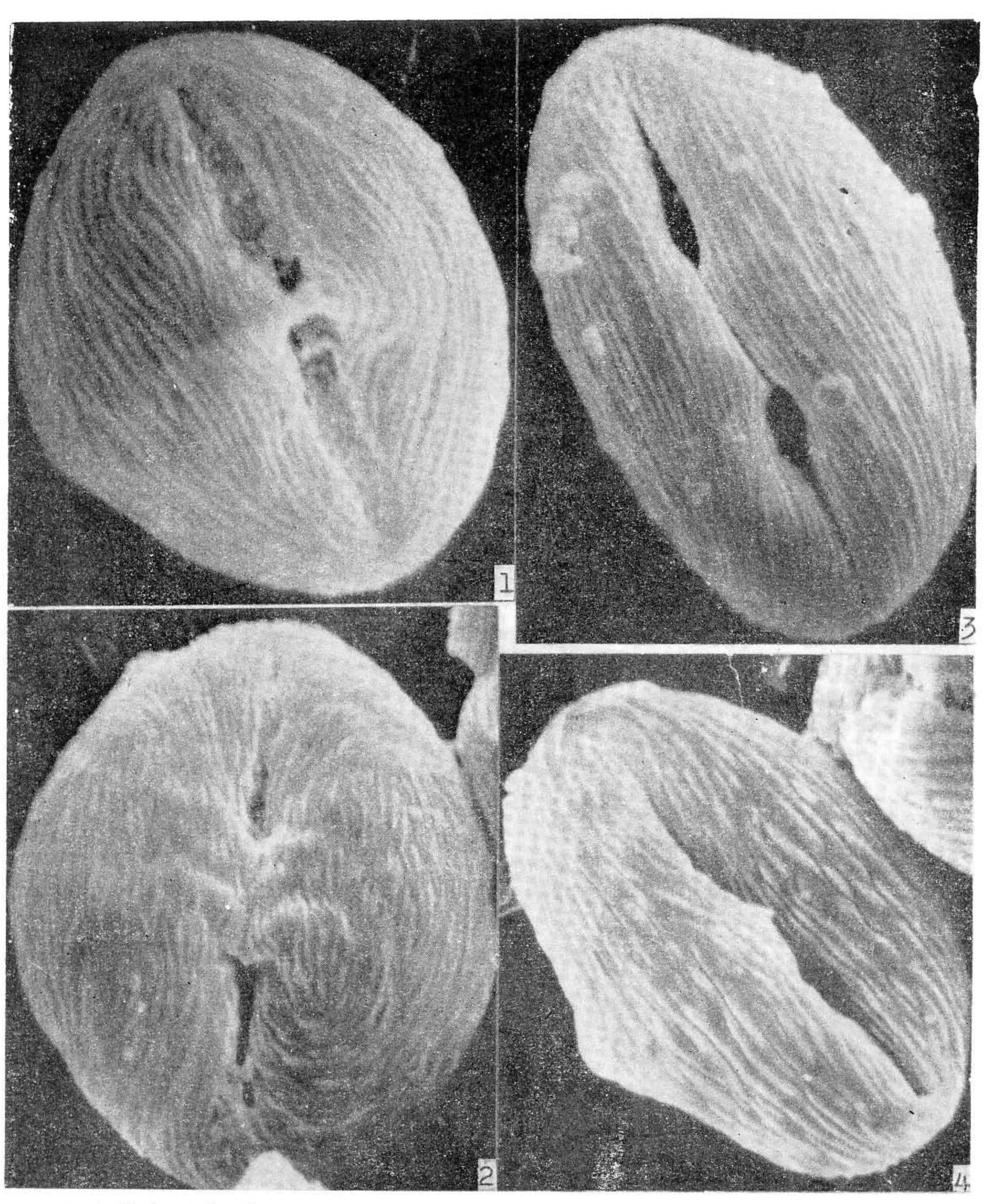
1—2.同工酶谱比较 Comparison of the peroxidase spectrum 1. *Taihangia rupestris* Yü et Li; 2. *Taihangia rupestris* var. *ciliata* Yü et Li; 3.太行花体细胞染色体 Somatic chromosomes of the *Taihangia* ×3750 (2n = 14); 4—15.花粉光学显微镜照片 Micrographs of pollen grains. 4—5. *Dryas octopetala* var. *asiatica* Nakai; 6–7. *Taihangia rupestris* Yü et Li; 8—9. *Acomastylis macrosepala* (Ludllow) Yü et Li; 10—11. *Geum rivale* L.; 12—13. *Waldsteinia geoides* Willd.; 14—15. *Coluria longifolia* Maxim. (4,6,8,10,12,14 极面观 polar view; 5,7,9,11,13, 15 赤道面观 equatorial view; all ×1000)



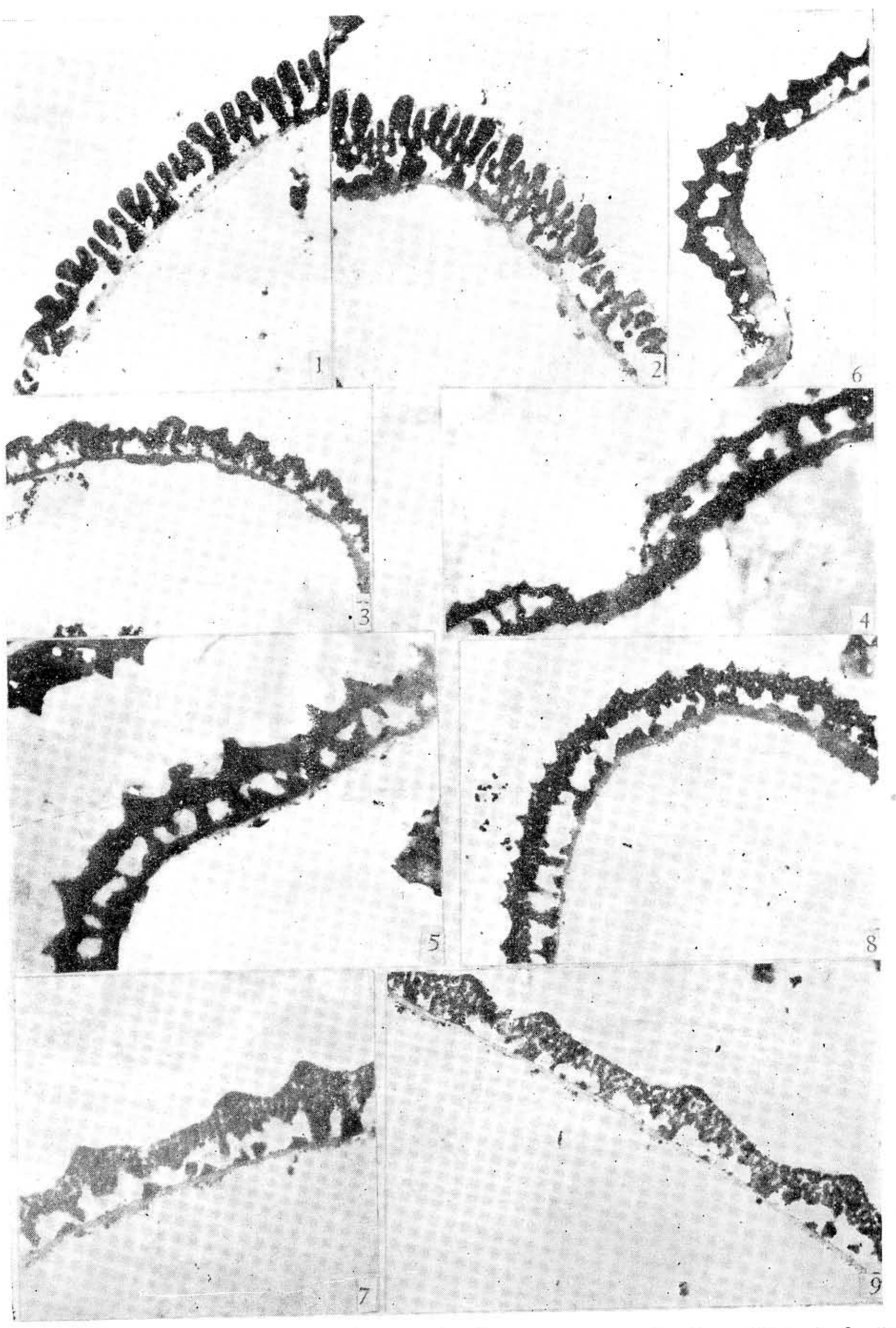
1—4. 太行花的花粉扫描电镜照片 SEM photographs of pollen grains of *Taihangia rupestris* 1—2. A 型花粉（示表面呈皱波状） A form, rugulate on the surface; 3—4. B 型花粉（示表面有短或长的条纹） B form, with short or long striae (1, 3. 赤道面观 equatorial view; 2, 4. 极面观 polar view; 1×3060; 2, 3, 4. ×3240)



1—4. 花粉扫描电镜照片　SEM photographs of pollen grains.　1—2. *Dryas octopetala* var. *asiatica* Nakai　1. A 型花粉(赤道面观)　A form, E. ×4200,　2. B 型花粉(极面观)　B form, P. ×3400; 3. *Acomastylis macrosepala* (Luddlow) Yü et Li,　赤道面观　E. ×3600;　4. *Acomastylis elata* var. *leiocarpa* (Evans) F. Bolle, 赤道面观　E. ×2160. E. = equatorial view; P. = polar view.



1—4. 花粉扫描电镜照片 SEM photographs of pollen grains. 1. *Geum rivale* L.，赤道面观 E. ×4300; 2. *Geum hispidum* E. Fries，赤道面观 E. ×4300; 3. *Waldsteinia geoides* Willd.，赤道面观 E. ×3400; 4. *Coluria longifolia* Maxim.，赤道面观 E. ×2890. E. = equatorial view; P. = polar view.



1—9. 花粉壁透射电子显微镜照片 TEM photographs of exine structure of pollen grains. 1—2. *Dryas octopetala* var. *asiatica* Nakai 1. A型 A form; 2. B型 B form; 3—4. *Taihangia rupestris* Yü et Li 3. A型 A form, 4. B型 B form; 5. *Geum rivale* L.; 6. *Geum urbanum* L.; 7. *Acomastylis elata* var. *leiocarpa* (Evans) F. Bolle; 8. *Waldsteinia ternata* (Steph.) Fritsch; 9. *Coluria longifolia* Maxim. (all ×10000).